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Tetradesmus, a new four-celled coenobic alga

GILBERT MORGAN SMITH

(WITH PLATE I)

METHODS AND MATERIAL

The alga described below was obtained during a study of various algae in pure cultures. The isolation of the different algae was by means of a medium consisting of 0.2% Knop's (9) solution and 2.0% agar in Petri dish cultures. By this method cultures were obtained which were the descendants of a single cell. Great care was used in the isolation, and only those cultures that were entirely free from other algae and bacteria were used in this study. After the isolation, cultures were made in sterile Knop's solution in 200 c.c. Erlenmeyer flasks. A complete description of the methods used will be given in a forthcoming paper.

The details of the cellular structure were studied in material which had been fixed in Flemming's weak osmic-acetic-chromic acid mixture diluted with an equal volume of water. For the washing and dehydration of the material a modification of Osterhout's (12) method was used. After the material had been allowed to stand in the killing solution for 24 hours, as much as possible of the solution was removed from the vial by means of a pipette, and then the vial was filled with distilled water. A celloidin film was prepared by pouring a celloidin solution on a clean surface of mercury and allowing it to harden so that it could be lifted up and placed over the mouth of the vial. The membrane was then allowed to harden still further while on the mouth of the vial. The material was then washed by simply placing it in a dish containing running water. For the purpose of dehydration the vial was transferred to 70 per cent. alcohol for 12 hours and then to two successive portions of 95 per cent. alcohol, at intervals of 12 hours. By means of this method the loss of material through decantation was obviated. The material was imbedded in paraffin and cut on a microtome into sections of from 3 to 5 μ in thickness.

The triple stain of Flemming gave the best differentiation, and all drawings are from preparations made in this manner.

I wish to express my thanks here to Professor Charles E. Allen for kind criticism and keen interest shown during the progress of this work and preparation of the manuscript.

DIAGNOSIS

The alga in question normally occurs in the form of four-celled colonies. The characteristic feature of the arrangement of the cells is that when viewed from the side they are seen to be in two tiers, while in *Scenedesmus*, apparently the most nearly related form, the cells are all in a single plane. The shape of the cells varies somewhat with their age, the mature ones being more ovoid. The following are the descriptions of the genus and species:

Tetradesmus gen. nov.

Colonies free, of 4 cells, rarely 1 or 2; cells in two planes, 2 cells in each plane, joined along the longer axes, ovoid with pointed ends; chlorophyl present throughout the cell, pyrenoid single. Reproduction by autocolonies inside of old cell wall, liberated by rupture of mother cell wall.

Coenobia segregata, e cellulis quaternis (rarius 1–2). Cellulae binae latere longiore in seriem duplicem conjunctae, ovoideae utroque polo acutae, homogeneae chlorophyllosae, et pyrenoide singulo praeditae. Propagatio fit autocoenobiis intra cellulam matricalem quae membranae ruptura prodeunt.

Tetradesmus wisconsinensis sp. nov.

Cells ovoid with sharply pointed ends, 4–5.8 by 12–14.5 μ.

HABITAT: Floating in sluggish streams and lakes; Madison, Wisconsin.

Cellulae ovoideae utroque polo acutae, 4–5.8 μ × 12–14.5 μ.

HABITAT: In rivulis lente fluentibus et lacubus libere natantes. Madison, Wisconsin.

The characters described above are sufficient, in my opinion, to warrant the assumption that we have a new genus. The objection may be made that this is merely a cultural form of *Scenedesmus acutus* Meyen; for according to Chodat (3), Chodat and Malinesco (4) (5), and Grintzesco (6), *Scenedesmus acutus* shows great variation under different cultural conditions. The regular arrangement of the cells in a linear series may disappear and the cells become isolated or arranged in the branching chain-like colonies which Naegeli (11) has described under the name of *Dactylococcus*. Although not at all conclusive, the fact is worthy of mention here that these investigators found no variation of *Scenedesmus acutus* which looked at all like *Tetradesmus*.

The alga in question has been under constant observation for over nine months and cultivated in different media, such as Knop's solution in different concentrations, Knop's solution with glucose or cane sugar, Beyerinck's (2) solution, and Knop's solution with 0.2–2% sodium chlorid. It has been cultivated under different conditions of illumination and temperature, and under none of these conditions has a colony been found with the cellular arrangement characteristic of *Scenedesmus acutus*. Conversely the evidence is just as strong, for I have had several different strains of *Scenedesmus acutus* under observation for the same length of time and under the same differing conditions, and in these cultures forms resembling *Tetradesmus* have never been found. If *Tetradesmus* were a cultural form of *Scenedesmus acutus*, the change from one form to the other should have been observed in this extensive series of cultures.

In the size, shape, and structure of the individual cells the two species also show constant differences. The cells of *Tetradesmus wisconsinensis* vary in size from 4–5.8 μ in width when the alga is grown in 0.1% Knop's solution; those of *Scenedesmus acutus* under the same conditions are 6.2–4.5μ in width. When the alga is grown in a 1.0% Knop's solution, the average diameter of the *Scenedesmus* cell increases to 6–7.8 μ, that of the *Tetradesmus* cell remaining practically unchanged. With the change to the stronger solution there is no change in the length of the individual cells. This change from the acicular to the ovoid-round shape of the cell in *Scenedesmus acutus*, when the concentration of the medium is increased, has been already pointed out by Senn (14). On the other hand, *Tetradesmus* shows no appreciable change in the shape of the cells when the concentration of the nutritive solution is increased. Beyerinck (1) and Senn (14) have shown that in weaker nutritive solutions the chromatophore of *Scenedesmus acutus* does not fill the entire cell but that there is a hyaline region at one side. My experiments with *Scenedesmus acutus* confirm this point; however, the chromatophore in *Tetradesmus* always completely fills the cell. The pyrenoid of *Scenedesmus* is constantly somewhat larger than that of *Tetradesmus*, being about 2.5 μ in diameter in the former and 1.5 μ in the latter. The arrangement of the starch grains differs somewhat, the characteristic segmentation of the grains around the pyrenoid being easily seen in *Scenedesmus* and only with great difficulty in *Tetradesmus*. In the older cultures of the former species the cell is usually filled with characteristic angular pieces of "stroma" starch that have been derived from the pyrenoid; in *Tetradesmus* kept under similar conditions the "stroma" starch granules are not very abundant. A good idea of the cellular structure of *Scenedesmus acutus* may be obtained from FIG. 3.

Among other coenobic algae the forms which appear to resemble *Tetradesmus* most closely are *Selenastrum* Reinsch (17) and *Lauterborniella* Schmidle (13). *Selenastrum*, as described by West (17), differs from *Tetradesmus* in that there are more than four cells in some of the colonies, and that the individual cells do not possess a pyrenoid. Dr. Schmidle has kindly compared my material with his type specimens of *Lauterborniella* and informs me that neither in size, shape, nor arrangement of the cells does *Tetradesmus* resemble *Lauterborniella*.

MORPHOLOGY

The individual cells of the *Tetradesmus* colony are always more or less ovoid, but in every case they are sharp-pointed at the ends. The cell wall is composed of two parts, as Chodat and Malinesco (4) have shown for *Scenedesmus*. The inner part is of cellulose and reacts to zinc chloriodid; the outer is composed of a gelatinous material which serves to bind the cells of the colony together. The existence of this outer gelatinous layer can be demonstrated by the use of some such stain as Bismarck brown. There is no central vacuole, but the entire cell except for the nucleus and the pyrenoid is filled with a cytoplasm which is granular or rarely slightly alveolar in structure. The chlorophyl is distributed throughout the cytoplasm and is not in the form of a definite chromatophore. Every cell possesses a single, eccentrically placed pyrenoid. In preparations stained with the safranin-gentian violet combination, the pyrenoid takes on a brilliant red coloration and the surrounding layer of starch is colored blue. The pyrenoid appears to be an entirely homogeneous body and not composed of lighter and darker regions, as Lutman (10) has shown to be the case in *Closterium*. On the other hand, the minuteness of the pyrenoid may possibly account for the failure to observe these details in its structure. A method devised by E. M. Gilbert, but as yet unpublished, in which a differentiation of the structure of the pyrenoid of *Sphaeroplea* was obtained by the use of safranin and Lichtgrün, was also tried, but no differentiation in the pyrenoid of *Tetradesmus* was observed. Surrounding the pyrenoid is a hyaline region which extends from the surface of the pyrenoid to the starch grains. This possibly may be a region that is composed of intermediate compounds in the formation of the starch grains, but this region failed to take any of the different stains used, although Timberlake (15) found that at times a part of it (in *Hydrodictyon*) stained with orange G. The starch granules surrounding the pyrenoid form a layer which is circular in outline and not angular as in *Hydrodictyon* (Timberlake) and *Closterium* (Lutman). FIG. 6 shows that there is some variation in the width of the starch layer and also that the outline of the starch ring may approach the ovoid but never the angular. The drawings also bring out the fact that the pyrenoid is not always in the center of the starch ring but may be towards one side. The starch layer is not a single unbroken ring but is composed of curved plates. FIG. 8 shows this segmentation of the starch layer. The determination of this point is an exceedingly difficult matter, although it may be noted again that the individual starch plates in *Scenedesmus* are easily observed. In the case of some of the older cells starch granules may be also found in the cytoplasm some distance from the pyrenoid (FIG. 7). These granules have been given the name of "stroma" starch by Klebs (8), but Timberlake (15) has shown that they are of pyrenoidal origin. The existence of the "stroma" starch may be taken as evidence of a somewhat pathological condition, since it is never found (at least in *Tetradesmus*) in any except the old, yellow-colored cultures. The "stroma" starch is also produced in much larger quantities in the *Scenedesmus* cell than it is in the *Tetradesmus* cell.

The nucleus is usually at the inner side of the cell (FIG. 1), but it as well as the pyrenoid may lie in the long axis of the cell (FIG. 2). Frequently the nucleus and the pyrenoid are symmetrically placed in the long axis of the cell. There is always a single nucleole within the nucleus. The chromatin seems to have a very fine granular structure, and the only apparent difference between the cytoplasm and the non-nucleolar part of the nucleus is the greater density of the latter when the material is stained with Heidenhain's iron-alum-hematoxylin.

REPRODUCTION

Reproduction always takes place by the formation of autocolonies within the mother cell wall. The formation of zoöspores or motile gametes was never observed. In this respect the form resembles *Scenedesmus*, whose sexual reproduction is unknown.

The division of the nucleus was not observed with certainty, on account of the minuteness of the nucleus, but stages in the cleavage of the cell were found in sufficient abundance to warrant the assumption that the following is the correct description of the process.

The nucleus divides so that the daughter nuclei lie in a line parallel to the long axis of the cell, as shown by a cell containing two daughter nuclei (FIG. 9). This stage was found in great abundance, and the two daughter nuclei were always found at the inner side of the cell. Following this division of the nucleus comes a cleavage of the cytoplasm, so that each half of the protoplasmic mass contains a nucleus (FIG. 10*A* and 10*B*). This division takes place by the formation of a cleavage furrow from the outside toward the center. The process seems to be similar to that observed by Harper (7) in the spore formation of certain fungi and by Timberlake (16) in the swarm spore formation of *Hydrodictyon*. The daughter cells resulting from this division are two naked protoplasts which lie close to one another and are not separated by a wall. The pyrenoid does not divide during this process; consequently, at the end of the first cleavage one daughter protoplast contains a pyrenoid and one does not. This fact can be determined with the greatest accuracy since the staining reaction of the pyrenoid makes it the most conspicuous structure in the cell. Hundreds of cells at this stage of development have been observed, and in every case the pyrenoid was easily distinguished in one of the daughter protoplasts while the other was empty. At first this cleavage without a division of the pyrenoid was thought to be an abnormality, but the abundance of cells in this condition and the failure to find a single case in which a pyrenoid appeared in each of the daughter protoplasts show that this is the normal condition.

The first plane of cleavage is usually approximately at right angles to the long axis of the cell (FIG. 10*A*), but soon after the cleavage the daughter protoplasts arrange themselves inside of the mother cell wall so that the original cleavage plane appears to be diagonal (FIG. 10*B*). The stimulus which leads to this twisting of one of the protoplasts upon the other is not known. A second division of the daughter nuclei now occurs. FIG. 11 shows this fully completed, the direction of the division, to judge by the position of the resting nuclei, always being parallel to the primary cleavage plane. There is some variation in the time at which this second division takes place; in some cases it occurs when the primary cleavage plane is only a few degrees from the transverse position, but in others the primary plane has come to lie at an angle of 45 degrees with its original position before the second nuclear division occurs. FIG. 11 shows that after the second nuclear division a single pyrenoid is still in evidence in one of the protoplasts while there is none in the other. The amount of starch surrounding the pyrenoid is approximately the same as that in the undivided cell, but this is not brought out in the figures, since material which is well stained for the nuclear structures does not show the starch about the pyrenoid. FIG. 10*B*, from material which was stained especially to bring out the pyrenoid, shows that after the first cell cleavage there is still considerable starch about the pyrenoid.

Following the second nuclear division there is a cleavage in each of the protoplasts. These cleavages seem to be usually simultaneous, but FIG. 12 shows a case in which the cleavage has been completed in one of the daughter protoplasts and not in the other. The relation of the cleavage planes to one another shows that there are certain mechanical factors governing their position. It is well known [Wilson (20)] that in the cleavage of the animal egg changes often occur in the position of the cells with regard to one another. Surface tension seems to be one of the factors governing this change. In moss rhizoids, de Wildeman (18) found that the cross walls are always S-shaped in section, so that although the cross wall as a whole is placed diagonally, yet its junction with the outer walls of the rhizoid is at right angles. This curving of the cleavage planes where they meet the mother cell wall occurs in substantially the same manner in *Tetradesmus* (FIG. 13, 14).

One view of the young four-celled colony, shortly after the second cleavage, when seen from the side, is shown by FIG. 13, but when the young colony is seen in a plane at right angles to that shown in this figure, we observe the very different appearance shown in FIG. 13*A*. FIG. 13 shows that even after the four protoplasts of the young colony are formed, one and only one contains a pyrenoid. At this stage, or very shortly after, the old pyrenoid disappears (FIG. 14). This disappearance probably takes place quite rapidly, since no intermediate stages were found between those shown in FIG. 13 and 14. In no case was the pyrenoid recognizable at stages later than those of FIG. 13 and 14.

The changes that follow in the young colony might be well said to constitute a period of maturation. The maturation consists in an elongation of each of the daughter protoplasts until it extends the entire length of the mother cell. The protoplasts do not elongate so as to lie in one plane, but the two in one (which we may call the lower) half of the cell slip up over the two in the upper half. This slipping occurs along the diagonal plane of the first cleavage. A stage in this slipping is seen in FIG. 15, although the drawing fails to bring out the fact that a portion of each of the two upper cells is hidden by part of the lower pair of cells. When this elongation is completed, the daughter cells are arranged in two planes, so that only two cells may be seen in any lateral view (FIG. 16). The growth of the four daughter cells seems not to be an equal elongation of all parts, but rather an elongation of the end of each of the daughter cells farthest from the corresponding apex of the old mother cell. As a result the nucleus of each daughter cell is not found in the center of the cell but nearer the end that was originally in contact with the apex of the mother cell wall. FIG. 15 shows this fact, but it must be borne in mind that a portion of the upper pair of cells is concealed by the lower ones. At the beginning of this elongation there is no pyrenoid present in any of the daughter protoplasts (FIG. 15). The further steps in the maturation of the daughter cells consist in the formation of pyrenoids and cell walls. The daughter cells are without pyrenoids until they have reached their full length, and then a pyrenoid suddenly appears in each (FIG. 16). Such an origin of pyrenoids *de novo* is contrary to the current conception, according to which a pyrenoid always arises by the division of a preëxistent pyrenoid but is in harmony, as will be later pointed out, with Timberlake's observations in *Hydrodictyon*. The formation of the new pyrenoid possibly may be a result of the metabolic activities of the nucleus, since the pyrenoid at its first appearance is often very close to the nucleus (FIG. 17). In other cases, possibly representing later stages, the pyrenoid is at a greater distance from the nucleus (FIG. 16). At about the same time as the appearance of the pyrenoid a cell wall is formed around each of the four protoplasts while they are still within the old cell wall.

The liberation of the daughter colony is through a longitudinal break in the mother cell wall. End views, such as those shown in FIG. 19 and 20, are especially favorable for studying the relation of the daughter coenobe to the mother cell wall. The opening through which the young colony escapes is a fissure that extends the whole length of the mother cell wall (FIG. 18). The cause of this rupture is probably the growth of the young colony within the old wall. It is not an irregular break but a definite longitudinal split, which is always at the side turned away from the other cells of the mother colony. After liberation the young coenobe is composed of cells which are of nearly full length but which are much more acicular than the mature cell (FIG. 17). The further history of the coenobe consists in the growth of the individual cells until they have assumed the shape characteristic of the adult stage.

DISCUSSION

Tetradesmus belongs to the family *Coelastraceae*, recently established by Wille (19). *Tetradesmus* shows a close relationship to *Scenedesmus*. The method of reproduction is essentially the same as that which occurs in *Scenedesmus*, the chief difference being that at the time of liberation from the mother cell wall the cells forming the coenobe in *Scenedesmus* become arranged in the form of a plate, while in *Tetradesmus* they remain rolled up. It seems probable that one form has been derived from the other, but there is little evidence as to the direction that the phylogenetic development has taken. There is also the possibility that these two forms have been derived from a common ancestor. *Tetradesmus* may have been derived from *Scenedesmus* through a loss of the tendency for the cells of the coenobe to unroll and spread out into a linear series after their liberation from the mother cell wall; or some colony of *Tetradesmus* may have developed this character of unrolling the cells in order to obtain an arrangement of the individual cells better adapted for photosynthesis.

Cytological study shows that these forms (*Tetradesmus* and *Scenedesmus*) are more closely related to *Hydrodictyon* and *Pediastrum* than has been usually supposed. In the last-named forms reproduction takes place by the formation of a more or less definite number of zoöspores, which then become arranged in the form of the mature colony while they are still inside the old mother cell wall or inside a gelatinous vesicle. In *Tetradesmus* and *Scenedesmus* there is a successive division into a definite number of uninucleate masses of protoplasm. These correspond to the zoöspores of *Hydrodictyon* and *Pediastrum* in every way except for the fact that they have no power of movement. We may easily think of these daughter cells in *Tetradesmus* and *Scenedesmus* as zoöspores which have lost the power of movement. The loss of power of motility of the zoöspores inside the mother cell wall is probably a step in advance of the condition in *Hydrodictyon*. There is also the possibility that this loss of movement of the zoöspores is connected with the smaller number of spores produced and the greater ease with which they get into their permanent positions. Reproduction in *Tetradesmus* is completed by a movement of the "zoöspores" into the position which they will occupy in the mature colony, and then by the liberation of the young colony from the mother wall.

Another similarity between the young daughter cells in *Tetradesmus* and the swarm spores in *Hydrodictyon* is in the behavior of the pyrenoid. In *Hydrodictyon*, Timberlake (16) noted that after the swarm spores are formed by cytoplasmic cleavage, new pyrenoids appear as small red-staining bodies closely associated with the nuclei. This is exactly what takes place in *Tetradesmus* and gives us a further basis for considering the young daughter cells of *Tetradesmus* the morphological equivalents of the swarm spores of *Hydrodictyon*. As in *Hydrodictyon* also, the daughter cells at first have no cell wall, but a cellulose wall is formed after the daughter cells have settled down into the position which they will have in the adult colony.

SUMMARY

1. *Tetradesmus* is a distinct genus, and not a cultural form of *Scenedesmus*.

2. Reproduction takes place by the formation of non-motile cells (spores) by successive nuclear and cell divisions. These spores then become arranged in the form of the adult colony while they are still inside the old cell wall. The young colonies are liberated by the rupture of the mother cell wall.

3. The pyrenoids in the daughter cells arise *de novo* and not by the division of a preëxisting pyrenoid.

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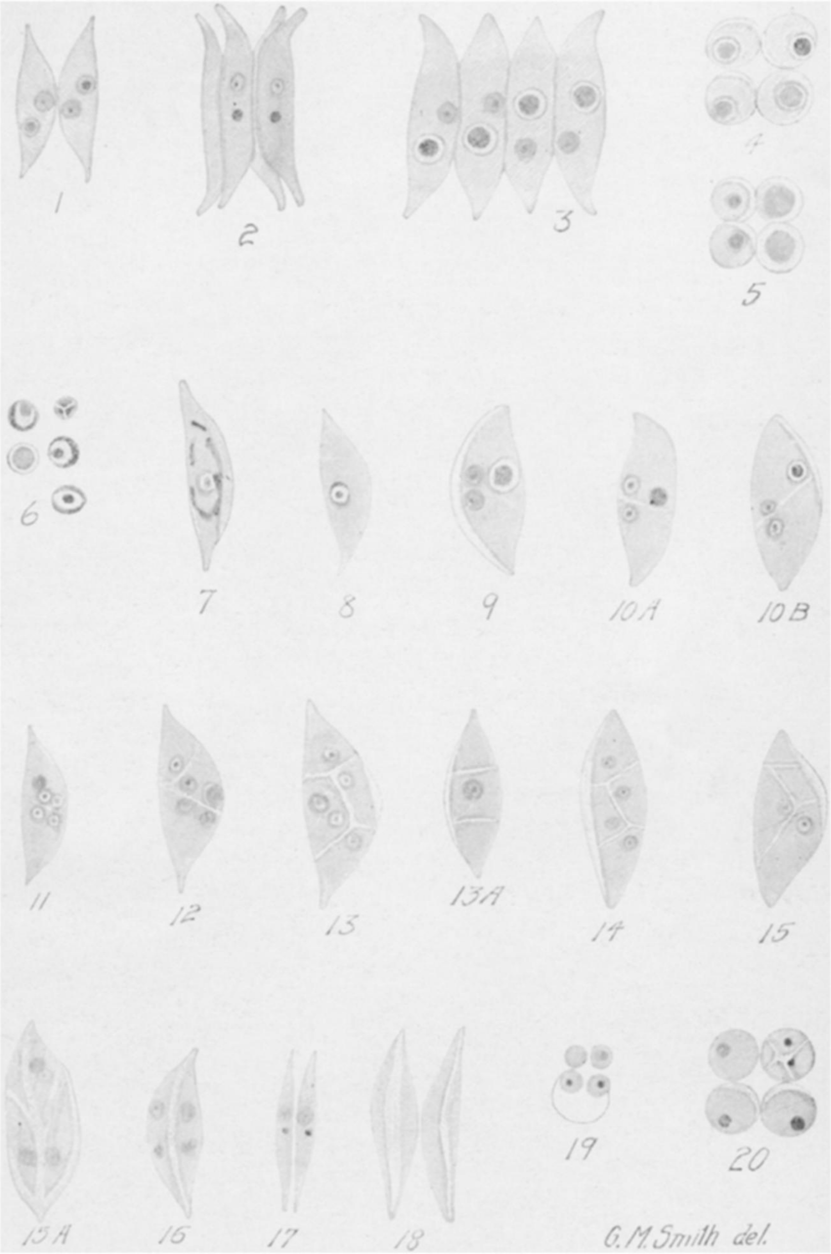
Explanation of plate I

All figures, with the exception of FIG. 3, are of *Tetradesmus wisconsinensis*. They were drawn with the aid of the Abbe camera lucida, the drawing being at the level of the base of the microscope, and with the Leitz objective 1/16 and ocular 4. The magnification is about 2,200 diameters.

FIG. 1. Longitudinal section of colony.

FIG. 2. Surface view of colony, showing arrangement of cells.

FIG. 3. Colony of *Scenedesmus acutus* Meyen grown under the same cultural conditions as the colonies of *Tetradesmus* shown in FIG. 1 and 2.



SMITH: TETRADESMUS

FIG. 4, 5. Transverse sections of colonies.

FIG. 6. Various forms taken by the pyrenoid and the surrounding starch layer

FIG. 7. Cell showing "stroma" starch granules.

FIG. 8. Cell showing the pyrenoid with segmented starch ring.

FIG. 9. A cell after the first nuclear division.

FIG. 10A, 10B. Completion of first cell division.

FIG. 11. After the completion of the second nuclear division.

FIG. 12–14. Stages in the second cleavage of the cytoplasm.

FIG. 15, 15A. Beginning of elongation of the four daughter cells.

FIG. 16. Young colony inside of mother cell wall (lateral view).

FIG. 17. Young colony, immediately after liberation from mother cell.

FIG. 18. Empty mother cell walls after liberation of young colonies.

FIG. 19. End view of daughter colony, showing method of its liberation from mother cell wall.

FIG. 20. Transverse section of coenobe, showing young colony within the wall of one of the mother cells.